

FLOOD FREQUENCY AND THE ASSEMBLAGE OF DISPERSAL TYPES IN HANGING GARDENS OF THE NARROWS, ZION NATIONAL PARK, UTAH

George P. Malanson¹ and Jeanne Kay²

ABSTRACT.—Hanging gardens of the Narrows, Zion National Park, Utah, are plant communities growing at permanent seeps on the canyon walls. The gardens are isolated from each other and from other plant communities by vertical expanses of sandstone. Gardens consist mostly of herbaceous species less than 1 m tall. Though not individually species-rich, the hanging gardens are diverse as a group, and very dissimilar.

This study considers two explanations of the heterogeneous distribution of species in hanging gardens. The assemblages of dispersal types in gardens of different spatial attributes and disturbance frequencies are examined. The G_{H1} statistic, a log likelihood ratio test, analyzes the incidence of dispersal types among classes of three spatial and two disturbance variables.

The disturbance variables of expected flood frequency and soil depth segregate dispersal types; and the spatial variables of area, distance to possible seed sources, and relative isolation do not. Ferns and mosses, dispersing through spores, dominate a heterogeneous fugitive guild in the flood-prone gardens. Infrequently flooded gardens support more large-seeded species.

Zion National Park of southwestern Utah is renowned for the sheer canyons of the North Fork of the Virgin River, which dissect over 600 m of Navaho sandstone. Compared to the arid and semiarid environments of the Colorado Plateau, the climate of the narrow canyons is cool and moist, and direct sunlight may penetrate for only a few hours per day. Large expanses of the canyon walls support no vegetation. Vascular plants, including shrubs and trees such as *Pinus ponderosa*, inhabit the occasional crevices. Perhaps the most beautiful plant communities of the canyon faces are the hanging gardens, which include ferns and wildflowers among their species. Hanging gardens are defined here as insular plant communities growing at permanent seeps on canyon walls (Fig. 1).

Seeps occur where precipitation has percolated downward through a porous formation until meeting less permeable strata, and it then flows laterally until a canyon intersects this plane. The volume of water discharged from permanent seeps in Zion Canyon varies from barely perceptible trickles to gushing springs. The seeps, and consequently the hanging gardens, assume a variety of shapes. Seeps usually create a less steep, relatively narrow ledge on the canyon wall. At

other sites, vertical jointing concentrates the seepage, or travertine deposits from calcium carbonate in the water create bulging forms. Relict potholes containing permanent seepage water supplies also support hanging gardens.

Hanging gardens illustrate several biogeographic problems. The effects of the unusual environments of hanging gardens on species composition have not been adequately explained. Also, the isolation of gardens by steep rock surfaces provides another testing ground for concepts of island biogeography. Most studies of island biogeography treat broad areas where pathways of dispersal between sites are not restricted (Simberloff 1974). The linear course of Zion Canyon, however, is an additional constraint on the movement of propagules between hanging gardens.

Earlier studies of hanging gardens (Welsh and Toft 1976, Nebeker et al. 1977), island biogeography (MacArthur and Wilson 1967, Diamond 1975), and plant distributions (Platt 1975, Levin 1976a, 1976b) suggest several explanations of the assemblages of hanging garden species. Species distributions are influenced by (1) habitat requirements and tolerances, (2) species' abilities to disperse to

¹Department of Geography, University of California, Los Angeles, California 90024

²Department of Geography, University of Utah, Salt Lake City, Utah 84112.



Fig. 1. A hanging garden in the Narrows, Zion National Park, Utah.

sites of different sizes and degrees of isolation, and (3) time elapsed since sites were opened by disturbance.

Few authors have investigated the vegetation of hanging gardens, and their conclusions emphasize the importance of habitat and isolation as controls of plant distribution. Woodbury (1933) outlined primary succession at seeps from algae to mosses and vascular plants. Welsh and Toft (1976) disclosed the geographical affinities of species they found at seeps of different morphology, calling hanging gardens "relictual refugia" of species not native to the region. Welsh and Wood (1976) studied structure, and Wood and Welsh (1976) measured productivity of hanging gardens, finding stability of both. Nebeker et al. (1977) examined floristic similarity, flower size, and dispersal type in hanging gardens, and concluded that the assemblages were "random assortments of individuals from the species pool capable of exploiting the environments of individual sites."

Malanson (1980) recently explored the relationships of species and habitat in hang-

ing gardens of Zion Canyon. Although the gardens were floristically dissimilar, species assemblages did not clearly vary according to perceptible differences in physical environment. Tests of species presence across a range of habitat and spatial variables produced few significant relationships. A few gardens had relatively high levels of solar radiation that might exclude several species. He also found a species-area relationship characteristic of small islands (Whitehead and Jones 1969).

Malanson (1980) concluded that other factors must influence assemblages of hanging gardens. This study examines the ideas that spatial characteristics and disturbance histories of the gardens affect the incidence of dispersal types, and thereby the plant assemblages.

METHODS

We sampled 29 of the 60 hanging gardens observed in an 8 km section of the Narrows and in 0.75 km of a tributary (Orderville

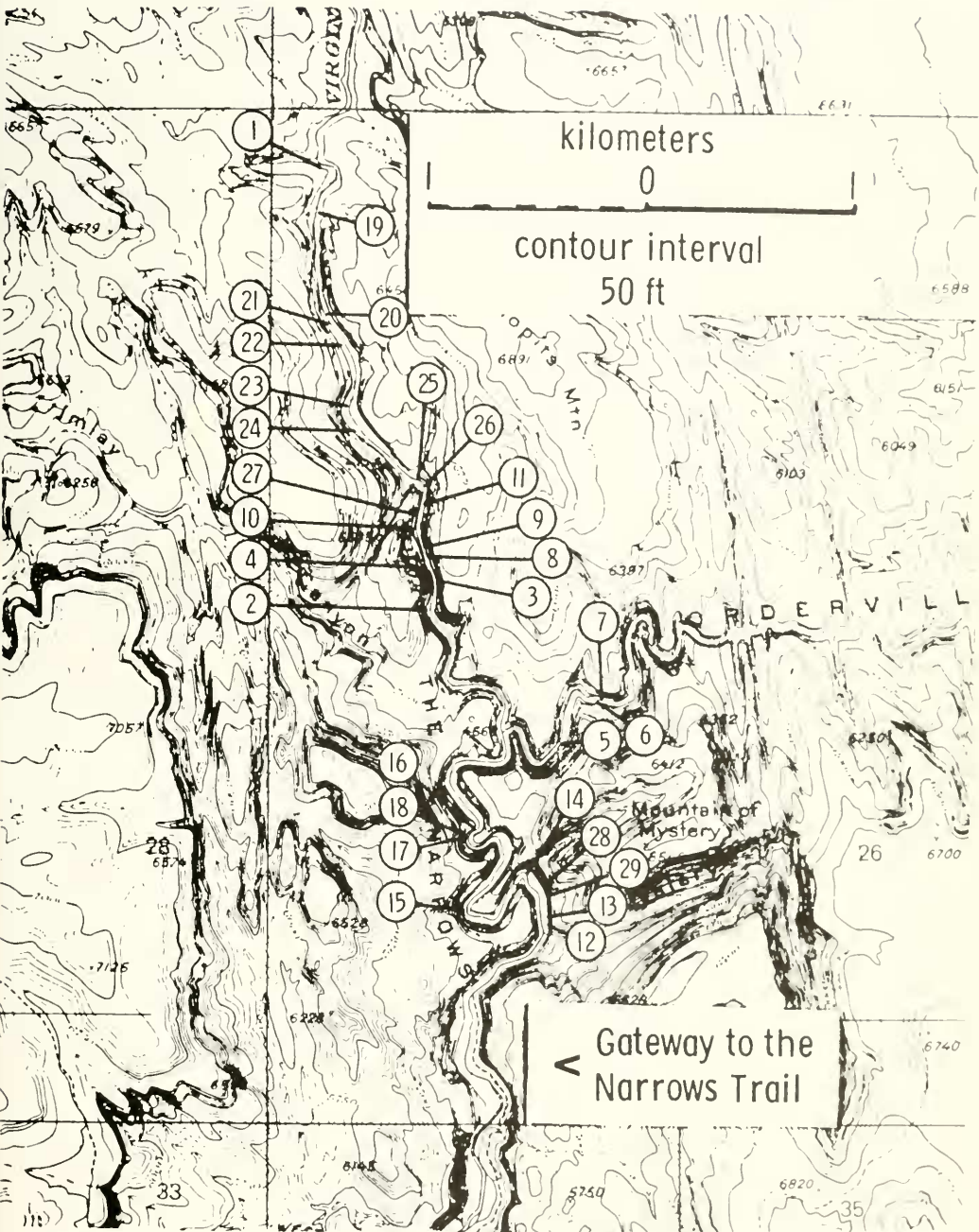


Fig. 2. The location of sampled hanging gardens and the topography of the Narrows.

Canyon) between June and September 1977 (Fig. 2). Sites were selected for approachability, though five were reached only through technical climbing, and for variety of garden sizes. Species presence was recorded along line transects spanning the breadth

of the gardens, spaced at 2 m intervals and perpendicular to the long axis. Species were identified in the field or at the Garrett Herbarium, University of Utah, and were subsequently classified according to dispersal type, according to Dansereau and Lems

(1957). Seed descriptions in floras of the western United States (Arnow and Wyckoff 1977, Davis 1952, Flowers 1973, Hitchcock and Cronquist 1973, Munz and Keck 1970) facilitated this classification. Malanson (1980) provides additional information on sample design.

We measured three spatial variables to test the applicability of island biogeographic hypotheses to the distribution of hanging garden species. These variables are (1) area of the gardens, (2) relative isolation from other gardens, and (3) distance of gardens from the terminus of the Gateway to the Narrows Trail. Area was derived from vegetation survey transects. Isolation is defined as the sum of the distances from each garden to its three nearest neighbors, as determined from a topographic map (ZNHA 1977). This arbitrary measure was suggested by the stepping-stone effect whereby species colonize one "island" from another (MacArthur and Wilson 1967). The terminus of the Gateway to the Narrows Trail coincides with the entrance to the Narrows (Fig. 2). The trail receives much pedestrian tourist traffic, but use declines markedly beyond it. The distance provides a crude index of gardens' accessibility to animal-dispersed or riparian species originating outside the Narrows environment.

Because flash floods are a common environmental disturbance of Zion Canyon, we evaluated the susceptibility of gardens to inundation. The discharge of the North fork of the Virgin River is recorded at a USGS gauge 10 km downstream from the Narrows. Maddox, Hart, and Hawkins (1977) calculated the expected return periods for instantaneous peak flows from magnitude and frequency data recorded at this gauge. After measuring the various canyon widths and elevations where hanging gardens are located, we estimated the probable frequencies of flooding for each garden. Two classes of flood frequency were used: less than 7.5 yr and greater than 15 yr. These classes should be distinct and allow some margin of error without overlap. We also measured soil depth, assuming that high-velocity floods would scour soil from affected gardens.

The G_{H1} statistic for heterogeneity (Sokal and Rohlf 1969) was used to disclose significant differences in the incidence of the four

TABLE 1. Incidence of tested dispersal types in classes of the variables and relationship of soil depth and flood frequency in hanging gardens.

Class		Spore	Dispersal Type			
			Wind	Plume	Fleshy	
Area (m ²)	0-10	21	10	4	3	
	10-25	19	11	5	2	
	25-50	14	8	4	0	
	< 50	19	28	12	12	
Isolation (m)	0-80	10	13	7	5	
	81-160	26	24	12	19	
	161-240	14	5	3	1	
	241-320	11	9	1	0	
	< 320	12	7	2	2	
Distance (m)	500-1630	11	25	9	5	
	1631-2760	8	6	1	0	
	2761-3890	23	11	5	0	
	3891-5020	21	12	9	8	
	5021-6150	10	4	1	4	
Soil depth (cm)	0-1	19	12	1	1	
	1-2	29	18	10	10	
	2-4	8	1	0	2	
	4-8	1	1	0	3	
	< 8	12	25	14	11	
Flood (yr)	< 7.5	51	23	12	14	
	> 15	20	25	11	12	
Soil depth (cm)						
		0-1	1-2	2-4	4-8	< 8
Flood (yr)	< 7.5	7	9	2	0	1
	> 15	1	1	0	1	4

most common dispersal types between classes of the spatial variables and soil depth (Table 1). Only spores, wind-blown, plumed, and fleshy types were abundant enough to provide meaningful tests. We used a probability of $p = .05$ for significance. Because we made multiple comparisons, the .05 chance of Type I error applies to the individual tests where $df = 3$, but the probability of "experiment wide error" is much higher. To limit experiment wide error to .05 we judged individual tests at $p = .001$ (Gabriel 1966). Single tests of dispersal type and of soil depth between the two flood frequency categories were made at $p = .05$.

RESULTS

Forty-eight species were counted in the 29 hanging gardens (Table 2). The frequency of species occurrence ranges from 1 to 17. Only 13 species were found in more than four gardens. The number of species per garden ranges from 2 to 20. The average richness is

TABLE 2. Hanging garden plant species.

Species	Frequency	Diaspore type
<i>Abies concolor</i>	1	heavy
<i>Acer negundo</i>	3	winged
<i>Adiantum capillus-reneris</i>	15	spore
<i>Adiantum pedatum</i>	6	spore
<i>Amaranthus albus</i>	1	heavy
<i>Anaphalis margaritacea</i>	4	plumed
<i>Apocynum cannabinum</i>	1	plumed
<i>Aquilegia</i> spp.	13	wind-blown
<i>Aralia racemosa</i>	12	fleshy
<i>Artemisia ludoviciana</i>	1	wind-blown
<i>Aster catonii</i>	8	plumed
<i>Berberis repens</i>	3	fleshy
<i>Brickellia grandiflora</i>	1	spiny
<i>Bromus ciliatus</i>	3	plumed
<i>Calamagrostis scopulorum</i>	5	plumed
<i>Cirsium arizonicum</i>	1	spiny
<i>Cystopteris fragilis</i>	17	spore
<i>Dodecatheon pulchellum</i>	9	wind-blown
<i>Dryopteris filix-mas</i>	2	spore
<i>Eleocharis</i> sp.	3	wind-blown
<i>Epipactis gigantea</i>	3	heavy
<i>Equisetum hyemale</i>	1	heavy
<i>Fraxinus velutina</i>	3	winged
<i>Galium aparine</i>	4	glandular
Hepaticae	10	spore
<i>Heuchera versicolor</i>	2	wind-blown
<i>Juncus</i> sp.	2	windblown
<i>Lobelia cardinalis</i>	3	wind-blown
<i>Mimulus cardinalis</i>	13	wind-blown
<i>Mimulus guttatus</i>	1	heavy
<i>Muhlenbergia andina</i>	1	wind-blown
<i>Muhlenbergia mexicana</i>	2	wind-blown
<i>Nasturtium officinale</i>	2	wind-blown
<i>Poa nevadensis</i>	2	wind-blown
<i>Rhus radicans</i>	2	fleshy
<i>Rubus leucodermis</i>	3	fleshy
<i>Rumex</i> sp.	1	wind-blown
<i>Salix</i> sp.	1	wind-blown
<i>Smilacina stellata</i>	7	fleshy
<i>Sphagnum</i> sp.	14	spore
Sphagnaceae	9	spore
<i>Taraxacum officinalis</i>	4	plumed
<i>Thalictrum fendleri</i>	2	wind-blown
<i>Viola</i> spp.	3	expulsive
unidentified #1	1	
unidentified #2	1	
unidentified #3	2	
unidentified #4	1	

7.3 species, but in the seven gardens found to be infrequently flooded the average is 12. These seven gardens contain 80 percent of the rare species. All but one species identified are perennial.

The sizes of the hanging gardens vary greatly, from 2 to 100 m among samples. Most values of isolation are low. Twenty-four gardens are less than 300 m from the nearest three neighbors. All but four distances from

sampled gardens to the Gateway to the Narrows trail are clustered between 500–2000 m and 3000–5000 m.

Nineteen sampled hanging gardens are within the range of flash floods with an expected recurrence interval of 7.5 yr. Only seven gardens are high enough on the canyon walls to escape flood crests with a 15 yr expected recurrence interval, and gardens 28 and 29 probably never have been inundated. Three gardens could not be put unequivocally in either class.

Individual tests at $p = .05$, $df = 3$ indicate a higher incidence of spore dispersal types in the smaller and more isolated gardens and a larger proportion of the heavier, plumed, and fleshy types in the larger and less isolated gardens. However, when applying the $p = .001$ level to limit the probability of Type I error within the groups, the statistic revealed no significant differences in the 26 spatial tests (Table 3).

Among the 10 soil depth tests, the G_{11} statistic indicated a significant difference in dispersal type between the shallowest (0–1 cm) and the deepest (8 cm) classes. The incidence of dispersal types and soil depths significantly differed between the two classes of flood susceptibility. The frequently flooded gardens usually have thin soils and a high incidence of spore dispersal types, and the heavier, plumed, and fleshy dispersal types and deeper soils are more common in the infrequently flooded gardens.

DISCUSSION AND CONCLUSIONS

The length of time seeps are available for colonization between disturbances seems an important control of plant assemblages. The mosses and ferns disperse by microscopic wind-blown spores and can establish themselves rapidly in recently flooded gardens. However, at least seven species disperse through spores, and a few individuals of other dispersal types do establish themselves in frequently flooded gardens, so garden communities are not necessarily similar. The postulated susceptibility of 65 percent of this sample to frequent floods may explain why spore-dispersed plants were the most common types. Nebeker et al. (1977) found bird-dispersed types to be most common in hang-

TABLE 3. Significant differences disclosed by G_H statistic ($p = .05$ or less) for incidence of dispersal types in categories of spatial variables, soil depth, and flood susceptibility and incidence of soil depth classes in categories of flood susceptibility.

					Probability of a Type I error among tests
<i>Area</i> (m ²)	10-25	25-50	< 50		
0-10	—	.05	.05		
10-25	—	—	—		
25-50	—	—	—		.40
<i>Isolation</i> (m)	81-160	161-240	241-320	< 320	
0-80	—	—	.05	—	
81-160		.05	.01	—	
161-240			—	—	
241-320				—	.80
<i>Distance</i> (m)	1631-2760	2761-3890	3891-5020	5020-6150	
500-1630		.01	.05	.05	
1631-2760		—	—	—	
2761-3890			—	—	
3891-5020				—	.80
<i>Soil depth</i> (cm)	1-2	2-4	4-8	< 8	
0-1	.05	—	.02	.001	
1-2		—	—	.05	
2-4			—	.01	
4-8				—	.80
<i>Flood</i> (yr)	< 15				
7.5	.05				.05
<i>Soil depth</i> (cm)	Flood	15			
Flood < 7.5	.01				.01

ing gardens of Arches and Canyonlands National Parks. Where garden habitats are seldom disturbed, large-seeded species are probably more successful competitors in plant succession, because their larger propagules provide more energy to their seedlings.

The term *hanging gardens* is useful from the standpoint of vegetation physiognomy, but it has little relevance to floristic composition and ecology. The species compositions of 29 hanging gardens in the Narrows of Zion Canyon were quite dissimilar, and variables of the gardens' physical environment do not afford a convincing explanation of the differences (Malanson 1980). Dispersal seems to be more important in influencing plant assemblages than the early successional environment represented by soil depth, because Malanson (1980) did not find many species limited by that variable.

The spatial variables of area, distance to a likely seed source, and relative isolation commonly are used by island biogeographers to predict species distributions. Hanging gar-

dens in the Narrows, however, are not demonstrably in equilibrium, and, without further investigation, we cannot support a spatial explanation of their plant assemblages.

Most species of the Zion Narrows could be considered "fugitive species" sensu Platt (1975), in being both perennial and comparatively vagile (annual colonizers are classified as "ruderals"). According to this method, following flash floods, the able dispersers would quickly occupy open spaces. During later stages of colonization, perennials would be more successful than annuals. Dispersal of annuals to a new site already occupied by perennials would have a low probability of success because of the scarcity of favorable spots. There may also be a high risk of seed loss from any established annuals, given the restricted habitat spaces available and the vertical nature of the Narrows environment. At the gardens situated above the flood crests, the fugitive species would give way to species with larger seeds.

A minority of seven gardens support the conclusion by Nebeker et al. (1977) that garden assemblages are "random" collections of plants. The majority of gardens in the Narrows apparently maintain their dissimilar, fugitive assemblages through response of dispersal types to frequent disturbance.

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